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The use of data-partitioning in the ordination and gradient analysis of a collembolan community

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With 3 figures

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1. Introduction

1.1. Ordination as a method of indirect gradient analysis

The continuum model of community organization assumes that individual species population densities are distributed according to unimodal, gaussian functions, and by continuous replacement along a single environmental gradient, form a corresponding coenocline (Whittaker 1978). Ordination techniques, such as Principal Component Analysis (PCA) and Reciprocal Averaging (RA), mathematically collapse a species by sample data matrix to a space of fewer dimensions. Indirect gradient analysis (*sensu* Gauch 1982) determines how well gradients of community composition, i. e. coenoclines, are represented by the abstract axes or components produced by ordination, and how well these axes or components are related to actual environmental gradients. While ordinations are useful in the context of delimiting relationships between communities of low beta diversity (*sensu* Whittaker 1978), and short portions of complex-environmental gradients, constraints of linearity and gradient "orthogonality" (*sensu* Gauch 1982) governing these eigenanalysis techniques may not be compatible with communities of high beta diversity. Swan (1970) recognized that coenoclines become increasingly convoluted in ordination space as the rate of species turnover, i.e. change in beta diversity, increases along an environmental gradient. The departure from linearity is spread among the second, third and higher level ordination axes as artifactual quadratic, cubic and higher order polynomial distortions of the first axis, respectively. Kendall (1975) and Fasam (1977) termed the phenomenon the "arch" or "horseshoe" problem.

Gradient "orthogonality" is the second problem facing community ecologists who wish to use ordination methodologies. However, PCA and RA may be rendered ineffective as trend-seeking methods for detecting relationships between species abundance data and underlying environmental gradients when the gradients are not independent of one another.

The linear structure of the principal component model can be more closely adhered to if data partitioning is employed prior to extraction of eigenvalues and eigenvectors. Data partitioning may obviate use of oblique (partially correlated) principal component rotation, since the biological importance of non-orthogonal solutions is not always clear (Gauch 1982). In an elegant application of the data-partitioning strategy to the fire history of subarctic woodland, Johnson (1981) separated temporal and spatial components in the vegetation dynamics by fitting species abundance data to a predominant gradient of fire recurrence to produce a successional ordination. A complementary habitat ordination (uncorrelated with the first) was constructed from the residual variation not accounted for by regression along the temporal fire frequence gradient.

1.2. The problem

Ordination has been frequently applied to species-rich microarthropod communities primarily as a transformation to reduce the high dimensionality of the data. Although microarthropods are arranged primarily along a gradient of soil moisture (e.g. BONNET *et al.* 1975; TODA & TANNO 1983), individual collembolan and acarine species are likely to be arranged along some other conspicuous macro-environmental gradient, such as vegetational composition, that covarie with soil moisture status (e.g. BLACKITH & BLACKITH 1975; CURRY 1977; PARR 1977; ADDISON 1980; PRAT & MASSOUD 1980; WAUTHY & LEBRUN 1980; PLOWMAN 1981a, b; POURSIN & PONGE 1982). Except within the simplest of communities (GODDARD 1979a, b; BOOTH & USHER 1984; WEST 1984), it has proved difficult, using ordination and indirect gradient analysis, to untangle the effects of soil moisture from more subtle influences of secondary gradients (e.g. soil pH, nutrient ion concentration) on soil faunal community structure (USHER 1976). In addition, obvious arch distortions present in the reduced ordination space may have a profound effect on subsequent interpretation of a few concurrently, but coarsely sampled environmental variables; Acari and Collembola are typically distributed below the scale attained by bulk measurement in a complex mosaic of microhabitat patches.

The purpose of the present study was to determine whether or not a data partitioning strategy could be successfully applied to gradient analysis and ordination of a species-poor collembolan community. The data for the analysis consisted of physico-chemical measurements and collembole species abundances which had been collected in the second field season (May to September 1980) of a 2-year study of soil faunal colonization of subalpine, reclaimed coal spoil. Data are also presented regarding the colonization of buried litter bag samples during the field season by microarthropods.

The species abundance data were resolved into linear and non-linear components of variation prior to ordination following the ideas presented by JOHNSON (1981). The first (non-linear) component relates species responses to a gradient of spoil moisture stress and its proxy variable spoil moisture content. This represented one aspect of the niches of the species involved in the ordination, i.e. extreme habitat adversity (*sensu* SOUTHWOOD 1977). Residual variation not accounted for by moisture was ordinated, and represents species response to a gradient of potential spoil erosion. This represented a second aspect of the niches of species ordinated, denoted by SOUTHWOOD (1977) as durational stability.

2. Site description

Three study plots (30 m × 50 m) were established on bituminous coal overburden which had been seeded as pasture by the reclamation division of Cardinal River Coals Limited, Luscar, Alberta. The three sites differed in age since initial reclamation (8, 4, and 2 years). Five 2 m × 10 m subplots were arranged, in turn, down the slope gradient within each plot. The ground cover was mostly vascular plant litter, underlain or supplanted by moss turf in poorly drained, low-lying areas of the plots. Surface runoff was intercepted by low spoil ridges (20 to 50 cm in height), spaced about 1 m apart, which ran discontinuously across the slopes, especially within the 2 year old plot. DURALL *et al.* (1985), and PARSONS & PARKINSON (1986) should be consulted for further descriptions of the region, and reclamation history of the subalpine study sites.

Each plot was surveyed in May 1979 to facilitate regular spacing of litter bags in an allied decomposition experiment (DURALL *et al.* 1985; PARSONS *et al.* 1986), and to provide topographic data for subsequent assessment of spoil erosional losses. The 1 mm mesh litter bags acted as crude sediment traps since burial of bags occurred with the onset of snow melt in 1980. Upslope angle, elevation (metres) above the toe of the slope, and aspect were recorded for each litter bag, and subsequently, for locations of spoil samples used in the present soil faunal study.

3. Methods

3.0. General

Three core samples (9.8 cm dia. × 5 cm) were collected at monthly intervals from each of the 15 subplots, May to September 1980 inclusive. The procedures describing sample preparation and measurement of physicochemical variables, as well as extraction, enumeration and identification of Collembola are outlined in PARSONS & PARKINSON (1986).

3.1. Analysis of complex-environmental gradients

3.1.1. Vegetation

A simple analysis of mine spoil vegetational development was performed by ranking the moss cover and the litter cover in 0.25 m^2 quadrats located over the core samples collected in the present study. The ascending ranks (0—6) corresponded to increases both in percentage areal cover and in the thickness of the litter layer or moss mat over mineral spoil. Combinations of the ranks assigned to the litter cover and moss cover data formed broad, but distinct groupings; these "vegetation classes" were used in subsequent correlation and regression analysis of spoil water potential. The same vegetation classes were also used as "treatment" levels in non-parametric ANOVA of sediment density, *p*H, slope angle, and soil organic matter data, as well as categories in subsequent Multiple Discriminant Analysis of the ordinated collembolan data (Section 3.2.). Slope angles were converted to slope classes (Anonymous 1978) prior to ANOVA.

3.1.2. Spoil water potential

Spoil moisture stress was measured at monthly intervals using calibrated psychrometric thermocouples (PT 51-10, Wescor Inc., Logan, Utah) attached to a dewpoint precision microvoltmeter (HR-33T, Wescor Inc.). The soil water potentials (ψ), expressed as positive values, were regressed against the ratio of actual volumetric spoil moisture content (Θ_v) to water content at saturation (Θ_s). Vegetation class, *p*H, organic matter, and USDA textural classes of percent sand, percent silt, and percent clay were included in the regression analysis. Volumetric moisture content at saturation was estimated as: $1 - (D_b/D_p)$, where D_b is sample bulk density and D_p is mean spoil particle density (2.34 g cm^{-3}). Spoil "water" or "moisture content" refers to the ratio $[\Theta_v/\Theta_s]$ in all subsequent analysis and discussion. All variables, except vegetation class and *p*H, were $\log_{10}$-transformed prior to regression analysis. Temporal differences in water potential were included in the regression analysis by coding months as "dummy" variables (PEDHAZUR 1982).

3.1.3. Spoil erosion

Spoil erosional losses were predicted using equations obtained by regressing $\log_{10}$-transformed density of spoil (g cm^{-2}, O.D.W.) trapped in the 20 cm $\times$ 20 cm 1 mm mesh litter bags against tan-(slope angle), and $\log_{10}$-transformed slope length (metres). Months in which the litter bags were sampled were coded as dummy variables. Mass losses of litter material in the bags and litter moisture content were rank correlated with actual sediment losses. Organic matter content, texture, moisture tension, and collembolan abundance and species composition of the spoil-infiltrated bags were also measured and correlated with sediment density.

Predicted sediment density (SED) was rank correlated with spoil water potential, *p*H, organic matter content, and vegetation cover data derived from the spoil cores taken within the subplots. The pairwise correlations were tested for homogeneity among months by computing Chi-square statistics on the normalized coefficients (SOKAL & ROHLF 1969).

3.2. Gradient analysis and ordination

Several attempts were made to relate variation in collembolan density to variation in physicochemical properties of Luscar spoil. In a direct gradient analysis (*sensu* WHITTAKER 1978), weighted averages of the untransformed collembolan abundance data were computed for each sample core, each month (May to September 1980). Ranks or weights averages assigned to each species corresponded to the order of increasing maximum species abundance along a gradient of increasing spoil moisture content as determined from data collected in the previous field season. During each month, samples were ordered as: $q_i = [X_{ij} * W_j]/X_i$; where q_i is the sample score for the ith core, W_j is the arbitrary rank given the jth species, X_{ij} is the abundance of the jth species in the ith core, and $X_{i.}$ is the total collembolan abundance of the ith core. The "q-scores" were rank correlated with the environmental variables.

Collembolan abundance data from the litter, 0 to 2.5 cm, and 2.5 to 5.0 cm strata were pooled, and transformed ($\log_{10}$ X + 1). Species occurring with a frequency of $\leq 4\%$ within each set of 45 monthly samples were excluded from trend surface and ordination analysis. The data remaining after the screen were standardized (by species) to normal scores.

Trend surface analysis (TSA) extends the least-squares regression criterion for fitting a line to data in two dimensions to the fitting or mapping of a surface in three dimensions (DAVIS 1973; UNWIN 1975). The simplest mapping function, a planar response surface, can be described by the first order multiple regression equation: $Z = b_0 + b_1 X_1 + b_2 X_2$, where b_0, b_1 and b_2 are partial regression coefficients associated with X_1 and X_2. Fitting of curvilinear surfaces is accomplished by polynomial expansion of the two independent variables in the initial first order equation.

In the present study, the normalized log-abundances of collembola were fitted by TSA to combinations of spoil moisture content and organic matter. Regression coefficients for first through fifth order surfaces were calculated using a FORTRAN program devised by DAVIS (1973). When

several regressions for a particular species yielded significant F-statistics, the equations were tested in pairwise fashion in ascending order (i.e. 1st vs 2nd, 2nd vs 3rd, etc.). The residuals about the response surface selected as the best fit were then ordinated.

R-mode principal components analysis (PCA) was implemented prior to, and after TSA, using the SPSS subroutine FACTOR (NIE *et al.* 1975). VARIMAX rotation was applied to the species ordinations in order to concentrate as much variation as possible onto the fewest number of principal component axes. In each monthly data set, core samples were considered as individual quadrats or stands. Factor scores for the stands were secondarily computed from the factor loading matrices for the species. The factor scores derived from PCA conducted on the data sets before TSA will be subsequently referred to as the "pre-TSA" stand ordinations. Factor scores obtained from PCA of the matrices of residuals remaining after TSA will be subsequented referred to as the detrended or "post-TSA" stand ordinations. For each month, factor scores for the first two principal components of the "pre-TSA" and "post-TSA" stand ordinations were rank correlated with water potential, water content, organic matter, *p*H, and predicted sediment density.

Factor scores for the first four principal components of the "post-TSA" stand ordinations were also subjected to Multiple Discriminant Analysis (MDA), with group membership based on vegetation classes. Linear discriminant functions were calculated using the SPSS subroutine DISCRIMINANT (NIE *et al.* 1975). Since equal sample size among groups could not be assumed, the Wilk's lambda likelihood ratio generated for the first discriminant function was used as a crude test of equality among multivariate means; the discriminant function coefficients are equivalent to coefficients used in multivariate analysis of variance (MORRISON 1976). The vegetation classes served as "treatment" levels in Kruskal-Wallis tests of the stand scores on the individual components. In addition, linear dependence of stand scores on vegetation class was examined by rank correlating the two variables.

4. Results

4.1. Vegetation classes

With the exception of *p*H in June, and water potential in August and September, there were significant differences among the vegetation classes with respect to mean levels of the other measured environmental variables (Table 1). All the environmental variables included in Table 1 were significantly correlated with vegetation class. Vegetation class decreased with increasing slope, very strongly so in May ($r_s = -0.84$, $p < 0.001$, $n = 45$), and to a lesser extent in the ensuing months (Chi square test of homogeneity of coefficients, $p > 0.05$; mean $r_s = -0.52$, $p < 0.001$, $n = 180$). Light moss cover ("lm") tended to be associated with high mean slopes (and therefore, high microrelief), independent of plot location. Similarly, light litter cover ("LL") was restricted to areas of high microrelief, which were subjected to greatest moisture stress, as evidenced by the low mean water potentials for "LLlm". Areas of low microrelief had both thicker litter layers and a more extensive moss turf; these areas had higher mean water potentials, soil organic matter and *p*H levels (Table 1). Predicted sediment density also differed significantly among vegetation classes for all months (Kruskal-Wallis test, $p < 0.001$); since sediment density could not be estimated for all plots, the significantly different mean rank sums from the non-parametric ANOVAs have been arbitrarily denoted "high", "medium", "low" and "very low" (see Section 4.3). Rank sediment density decreased linearly with increasing vegetation cover (Chi-square test of homogeneity of coefficients, $p > 0.05$; mean $r_s = -0.69$, $p < 0.001$).

4.2. Components of spoil water potential

The lowest (i.e. most negative) water potentials coincided with the lowest spoil moisture content measured during the 1980 field season in May. DILLON (1973), in an earlier study of plant germination success at Luscar, observed that a period of soil moisture deficiency occurred immediately following April to May snowmelt. Results obtained in the present study confirmed his prediction; in mid-May, water potentials in the 0 to 5 cm stratum of Luscar spoil averaged -1.37 ± 0.19 MPa on the 8 year old plot, -5.44 ± 0.18 MPa on the 4 year old plot, and -4.06 ± 0.46 MPa on the 2 year old plot (W. F. J. PARSONS, personal observation).

Frequent, light rain likely lessened moisture stress on all three plots towards mid-summer, as evidenced by increases in both mean water potential and mean moisture content (Table 2).

Table 1. Kruskal-Wallis tests of edaphic variables according to vegetation classes assigned to sample cores, May to September 1980

Month		Vegetation Class[1])					Kruskal-Wallis		
		LLlm	MLlm	MLmm	HLlm	HLmm	K statistics		r_s[2])
May	ψ	-4.31^{b}	-3.29^{ab}	-1.42^{a}	-1.22^{a}	—	174.74		−0.44
	SOM[3])	3.75^{a}	3.87^{a}	8.19^{c}	6.45^{b}	—	21.60		0.47
	*p*H	7.25^{c}	6.69^{b}	6.48^{a}	6.73^{ab}	—	21.19		0.72
	Slope[4])	5.3^{c}	3.4^{a}	4.1^{b}	2.9^{a}	—	45.35		−0.84
	Sed[5])	High	Med	Low	Low	—	17.07		−0.67
June	ψ	—	—	—	—	—	—		—
	SOM	3.64^{a}	3.48^{a}	4.01^{a}	5.43^{b}	5.76^{b}	9.71		0.39
	*p*H	6.94	6.61	6.57	6.57	6.78	7.22	NS	−0.43
	Slope	5.8^{c}	5.5^{c}	3.9^{b}	3.9^{b}	2.7^{a}	12.90		−0.51
	Sed	High	Med	High	Low	Low	32.59		−0.66
July	ψ	-1.42^{b}	-0.65^{ab}	-0.37^{ab}	-1.13^{ab}	-0.32^{a}	12.08		−0.50
	SOM	3.90^{a}	4.48^{bc}	3.98^{ab}	6.37^{d}	5.06^{c}	10.05		0.50
	*p*H	7.06^{c}	6.50^{a}	6.74^{b}	7.00^{c}	6.49^{a}	18.77		−0.58
	Slope	5.9^{c}	5.1^{bc}	4.6^{b}	3.0^{a}	3.3^{a}	15.23		−0.55
	Sed	High	Med	Low	Low	Low	22.14		−0.67
August	ψ	−1.29	−1.08	—	−0.83	−0.70	4.34	NS	−0.31
	SOM	3.11^{a}	3.91^{b}	—	4.97^{c}	5.18^{d}	10.29		0.43
	*p*H	7.08^{c}	6.53^{a}	—	6.89^{b}	6.77^{b}	9.50		−0.39
	Slope	6.1^{c}	4.5^{b}	—	3.4^{a}	3.3^{a}	20.57		−0.62
	Sed	High	Med		Low	Low	171.24		−0.69
September	ψ	−0.57	0.50	−0.22	−0.11	−0.44	5.42	NS	−0.35
	SOM	3.58^{ab}	2.78^{a}	3.56^{b}	5.50^{c}	5.91^{d}	11.64		0.34
	*p*H	7.03^{c}	6.79^{b}	6.68^{a}	6.82^{b}	6.76^{ab}	12.48		−0.31
	Slope	5.7^{c}	4.7^{b}	4.5^{b}	2.7^{a}	3.6^{a}	14.52		−0.42
	Sed	High	Med	V. Low	Low	V. Low	24.32		−0.75

1. Upper case letters refer to Light (L), Medium (M), and Heavy (H) litter cover, lower case letters, to light (l), medium (m), heavy (h) moss cover, corresponding to designations assigned to stand clusters in Figs. 2 and 3. Means in each row superscripted by the same letter do not differ significantly at $p = 0.05$, as determined from Kruskal-Wallis non-parametric ANOVA and *post hoc* contrasts. K-statistics that do not exceed critical Chi-square values are denoted "NS".
2. Spearman rank correlations (r_s) between the edaphic variables and vegetation classes are significant at $p = 0.05$.
3. SOM — percentage soil organic matter.
4. Slope class
5. Predicted sediment density. "Med" — medium, "V. Low" — very low.

Typical water potential values of −2.0 MPa to −0.1 MPa were obtained during the period of initial spoil moisture deficit. However, possibly as a consequence of collecting samples immediately following an extensive period of rainfall (late-May to mid-June), 33% of the June water potential readings fell outside the reliable range of the instruments employed in the determinations. Even after elimination of these measurements from the June data set, the regression equation water potentials from percent spoil moisture content was not significant at $p = 0.05$, and therefore, has not been included in Table 2. However, there were significant differences between months as indicated by Scheffé tests of the dummy variables included in the preliminary regression analysis, and as indicated by the magnitude of the standard errors of the monthly regressions, and the partial regression coefficients (Table 2).

Water potential and water content were significantly and inversely related (product-moment correlations, $p < 0.001$, $n = 45$) in May ($r = -0.73$), July ($r = -0.74$), August ($r = -0.83$), and September ($r = -0.55$). However, simple linear functions of water content, together with additive or multiplicative combinations of the other environmental variables, were not sufficient to predict moisture availability (spoil water potential) over the wide range of conditions present on Luscar spoil. Trend surface analysis of the water potential data was also not useful in this regard. Power functions (as depicted in Table 2)

Table 2. Moisture release curves based on of log-transformed psychrometric water potential versus log-transformed spoil moisture and organic matter content, May to September 1980

Month	Regression Coefficients (± SE)						Water Content (%)	Water Potential (MPa)
	b_0	b_1	b_2	R^2	F	SE_b		
May	1.45 (0.09)	1.05 (0.14)	0.41 (0.14)	0.77	70.90	0.22	6.60 (1.10)	—3.63 (0.31)
June	—	—	—	—	—	—	15.96 (1.00)	ND
July	1.94 (0.15)	—1.76 (0.12)	—	0.82	199.39	0.21	14.23 (1.09)	—1.26 (0.13)
August	2.80 (0.20)	—2.42 (0.16)	—	0.85	233.80	0.22	17.79 (1.08)	—1.07 (0.13)
September	2.41 (0.15)	—2.07 (0.09)	—	0.92	497.25	0.20	36.51 (1.20)	—0.51 (0.12)

Linear regressions of 45 replicate measurements per month are significant at $p = 0.001$. SE_b is the standard error of the regression.

Note:

b_0 Y-intercept, the air-entry coefficient of the spoil ($\log_{10}$ MPa) at 1% moisture and 1% organic matter content.

b_1 partial regression coefficient, $\log_{10} [\theta_v/\theta_s]$.

b_2 partial regression coefficient, $\log_{10}$ (soil organic matter).

ND Water potentials measured in June have been excluded from the regression analysis.

were the most efficient means of detailing relationships between water potential and the other physico-chemical variables; most of the variation in $\log_{10} \psi$ was accounted for by either $\log_{10}$ (water content) alone, or $\log_{10}$ (water content) plus $\log_{10}$ (organic matter). Inclusion of other $\log_{10}$-transformed variables did not significantly increase the variance explained by regression. Regression analysis using the untransformed variables required estimation of 4 or more regression coefficients, and explained a smaller proportion of the variance. The power function equations summarized in Table 2 were also consistent with empirical models of soil water relations devised by soil physicists (*cf.* HILLEL 1971).

Progressive weathering and settling of the Luscar spoil likely altered the spoil moisture retention characteristics, and subsequently, the moisture release curves summarized in Table 2. There was a significant increase (2-way ANOVA $F_{4,48} = 13.77$, $p < 0.001$) in bulk density from a mean 1.17 g cm^{-3} in May to 1.54 g cm^{-3} in September 1980. Consequently, mean available pore space decreased from 50 to 34% of total core volume. The decrease in pore space may explain the apparent increase in spoil moisture content through time, even though volumetric moisture content (Θ_v) progressively decreased over the field season (W. F. J. PARSONS, personal observation).

4.3. Litter bag burial and microarthropod colonization

Although spoil erosion was evident on the 8 and 4 year old plots during 1980, there were not enough litter bags to estimate sediment density on the two plots using least-squares regression. Actual sediment densities measured on the 8 and 4 year old plots were very low, usually < 100 mg m^{-2}. Predicted sediment densities on the two older plots were estimated by interpolating between grid locations with known sediment densities. Regression analysis was only used on data obtained from the 2 year old plot; there were no significant differences (Scheffé tests, $p > 0.05$) in mean sediment density among months on the 2 year old plot. Actual sediment displacement and redeposition amounted to 6.74 t ha^{-1} mo^{-1} ($\pm 1.34 \times 10^{-3}$ t ha^{-1} mo^{-1}) as determined from the litter bag measurements averaged over 4 months.

The depth to which litter bags were buried by spoil was reflected in the moisture content of the sediments. Actual sediment density was significantly correlated ($p < 0.001$, $n = 60$)

with sediment moisture content ($r_s = 0.85$), litter mass losses ($r_s = 0.70$), and the organic matter content of the sediment ($r_s = 0.57$) during every month of 1980 when litter bags were collected. The commonest microarthropods colonizing the buried litter bags, the collembolan *Hypogastrura denticulata* (BAGNALL), were significantly correlated with sediment density ($r_s = 0.68$) and sediment moisture content ($r_s = 0.67$). A second hypogastrurid, *Hypogastrura manubrialis* group *cf. brevispina* (HARVEY), was also significantly correlated with sediment density in July and September 1980 (mean $r_s = 0.61$, $p < 0.001$, $n = 40$).

Increased collembole densities with increased sediment density reflected an amelioration of moisture stress on Luscar spoil. The moisture content of the spoil-infiltrated litter bags was 30 to 40% (O.D.W.), four to ten times higher than moisture contents of spoil cores taken from the surrounding subplots on the 2 year old plot. Typical water potentials measured on the spoil cores collected from the 2 year old plot ranged from —3.6 MPa to —10 kPa throughout the field season. Water potentials of the sediments (calculated from pressure plate determinations) varied between —0.1 MPa and —15 kPa (W. F. J. PARSONS, personal observation).

Germination success of grass and legume seed was enhanced by the placement of litter bags on the 2 year old plot, especially where litter bags were buried. Larger numbers of viable seedlings germinated immediately under litter bags than from seed sprouting next to those bags. The spoil in and under the litter bags served as loci for enhanced plant growth and microarthropod colonization since spoil moisture and temperature conditions were likely ameliorated. Rooting grasses were found in most litter bags on the 2 year old plot 16 months (September 1980) after placement in the field. Although the abundance of *H. denticulata* extracted from these bags was not significantly different from abundances recorded for those bags without roots (Mann-Whitney U-test, $U = 22$, $p > 0.20$, $n = 18$), the organic matter content of the buried bags containing roots was significantly higher (Mann-Whitney U-test, $U = 72$, $p < 0.005$, $n = 18$). The population density of *H. denticulata* was significantly correlated, in turn, with organic matter content of the bags ($r_s = 0.58$, $p < 0.02$, $n = 18$). *Hypogastrura denticulata* and *H. manubrialis* were probably opportunistic, or fugitives species as suggested by the spatio-temporal variation in the litter bag colonization data.

Slope angle (α) and slope length (L) explained 50.5% of the variation in the sediment density data ($F_{2,57} = 29.10$, $p < 0.001$). The multiple regression equation predicting monthly downslope sediment loss and redeposition on the 2 year old plot was:

$$\log_{10} \mathrm{SED} = 3.96\,(\pm\, 0.54) * \mathrm{Tan}\,\alpha + 0.64\,(\pm\, 0.21) * \log_{10} \mathrm{L}$$

(The Y-intercept term did not significantly differ from zero, and therefore has not been included in the equation.)

Ranked predicted sediment densities, SED, were consistently (Chi-square test of homogeneity, $p > 0.05$) and inversely correlated from month to month with soil organic matter content (mean $r_s = -0.53$, $p < 0.001$, $n = 225$), and vegetation class (mean $r_s = -0.69$, $p < 0.001$, $n = 225$). Organic matter data derived from analysis of the spoil-infiltrated litter bags were too few to be useful in the regression analysis. Vegetation class was excluded from regression analysis as well since it varied little from the condition of LLlm ("light litter-light moss").

Predicted sediment density was significantly rank correlated in May, July, August, and September with spoil water content (mean $r_s = -0.45$, $p < 0.001$, $n = 180$) and water potential (mean $r_s = -0.53$, $p < 0.001$, $n = 180$); during June, the correlation between sediment density and moisture content was positive and not significant ($r_s = 0.22$, $p > 0.05$). Similarly, *p*H was not consistently correlated with predicted sediment density. The mean correlation between the two variables, averaged for May, July, and August, was $r_s = -0.54$ ($p < 0.001$, $n = 135$). The number of species present in the soil cores was inversely proportional to predicted sediment density in May, July, August and September (Chi-square test of homogeneity, $p > 0.05$; mean $r_s = -0.45$, $p < 0.001$, $n = 180$). The correlation of

species number and sediment density was not significant in June. However, total Collembola abundance and sediment density were significantly and positively correlated in June ($r_s = 0.3561$, $p < 0.02$, $n = 45$), but negatively correlated in May ($r_s = -0.36/0.48$, $p < 0.002$, $n = 45$).

High correlations with vegetation class, moisture content and organic matter suggested that SED was related to the erodibility factor K in the University Soil Loss Equation (WISCHMEIER & SMITH 1978). Predicted sediment density was not a measure of erosion hazard or annual soil loss *per se*, since neither standard test conditions were used nor were rainfall intensity, duration and frequency known. Knowledge of these factors is critical in calculating erosional losses using the USLE equation; however, the equation developed in the present study incorporated two basic elements of the USLE, i.e. slope length and slope gradient.

Present annual rates of erosion were conservatively estimated at 8,088 t km^{-2}, much lower than the 17,000—40,000 t km^{-2} y^{-1} predicted by MCKENZIE & STUDLICK (1979) who used the Universal Soil Loss Equation to measure erodibility of mine spoil banks in Ohio. Their predictions were based on sites with 30° to 35° slopes that had undergone 20 years of erosion, and where the eroding substrate consisted mainly of sand (64% by total sample mass).

4.4. Gradient analysis and ordination

Fourteen species of Collembola were collected from Luscar mine spoil over 2 years of study: *Arrhopalites principalis* STACH, *Bourletiella sp.*, *Hypogastrura denticulata* BAGNALL, *H. manubrialis* near near *brevispina* (HARVEY), *Folsomia nivalis* (PACKARD) *ssp. duodecimsetosa* HAMMER, *F. quadrioculata* (TULLBERG), *Isotoma ekamani* FJELLBERG, *I.* cf. *manitobae* FJELLBERG, *I. cf. tigrina* NICOLET, *I. viridis* BOURLET, *Metisotoma grandiceps* REUTER, *Onychiurus subtenuis* Folsom, *Tullbergia sp.* and *Entomobrya marginata* (TULLBERG). The "q-scores" (i.e. direct gradient analysis) derived from the abundance data for these species were significantly and negatively correlated with soil organic matter in June, July

Table 3. Summary of Trend Surface Analyses for collembolan species on Luscar mine spoil, May to September 1980

Species	May		June		July		August		September	
Hypogastrura denticulata	1,110	(27, 6.5)	1,980	(12.5, 4)	—		—		4,385	(16, 2.5)
		—	5,175	(26, 7.5)	—		—		4,380	(33. 6)
				—	—		—		4,380	(83, 4)
	3	(0.65)	4	(0.70)	—		—		5	(0.88)
Hypogastrura manubrialis		—		—	—		—		210	(0, 0)
		—		—	—		—		1	(0.39)
Folsomia nivalis	2,990	(27, 6.5)	625	(4, 7.5)	—		—		—	
		—	3,455	(12, 7.5)	—		—		—	
	3	(0.79)	4	(0.77)	—		—		—	
Onychiurus subtenius	1,000	(21, 5)	790	(11, 7)	1,625	(20, 6.5)	670	(27, 8)	2,590	(58, 5.5)
		—	1,795	(23, 7)	4,990	(55.5, 6.5)	10,955	(46, 10)	1,545	(69, 4.5)
	5	(0.79)	5	(0.83)	5	(0.95)	2	(0.64)	5	(0.90)
Isotoma cf. manitobae	200	(17.5, 7.5)		—	1,140	(28, 1)	—		—	
	200	(32.5, 10)		—		—	—		—	
	5	(0.83)		—	2	(0.63)	—		—	

For the sake of clarity, the regression coefficients defining the response surfaces are not shown, only peak densities (individuals per m^2), co-ordinates of the peaks (S, SOM), orders of significant surfaces, and the correlation coefficients of the equations are included. Correlations significant at $p = 0.05$ are singly underscored, and doubly underscored at $p = 0.01$.

Table 4. Spearman rank correlations of 5 environmental variables with the first and second principal component scores of the "pre-TSA" (NP) and "post-TSA" (P) stand ordinations, May to September 1980

Month		Moisture content	Organic matter	pH	Predicted sediment density	Water potential
May	NP I	0.39	0.38	—0.42	—0.59	—0.55
	II	0.10	—0.05	—0.28	—0.09	—0.03
	P I	—0.04	—0.08	—0.45	—0.04	0.06
	II	0.07	—0.07	0.05	0.12	—0.04
June	NP I	0.23	—0.04	0.37	0.54	—
	II	—0.12	0.48	0.15	—0.25	—
	P I	0.07	0.05	—0.13	—0.21	—
	II	0.15	—0.12	0.26	0.50	—
July	NP I	0.30	0.22	—0.51	—0.62	—0.29
	II	—0.22	0.05	0.26	0.42	—0.20
	P I	0.19	0.06	—0.40	—0.51	—0.19
	II	—0.21	—0.03	0.26	0.37	—0.22
August	NP I	—0.21	—0.19	0.08	0.35	0.31
	II	0.17	0.28	—0.35	—0.40	—0.09
	P I	—0.20	—0.20	0.15	0.43	0.23
	II	0.05	0.18	—0.28	—0.28	0.04
September	NP I	0.37	0.24	0.02	—0.45	—0.34
	I	—0.17	—0.10	0.28	0.43	0.19
	P I	—0.03	0.03	0.08	0.31	0.0I
	II	0.11	—0.04	0.06	—0.13	—0.07

Note: Underscored correlations are significant at p = 0.05

Table 5. Separation of stand scores by vegetation class for the first four "post TSA" principal components, both individually and as a group

Month		"post-TSA" Principal Components				Wilks' lambda	Chi-square
		I	II	III	IV		
May[1])	K	5.686 NS	7.456 NS	5.213 NS	2.485 NS	0.406	34.30 $p < 0.01$
	r_s	0.14	0.04	0.09	0.12		
June[2])	K	19.225	30.456	5.468 NS	5.334 NS	0.355	43.24 $p < 0.01$
	r_s	0.16	—0.67	0.35	—0.19		
July[2])	K	42.041	7.685 NS	4.612 NS	6.058 NS	0.406	36.35 $p < 0.01$
	r_s	0.48	—0.32	0.08	0.07		
August[1])	K	6.566 NS	7.869	3.794 NS	2.464 NS	0.485	28.98 $p < 0.01$
	r_s	—0.25	0.34	0.16	0.21		
September[2])	I	2.484 NS	12.957	8.795	2.646 NS	0.319	46.25 $p < 0.001$
	r_s	—0.15	0.29	0.29	0.07		

Note: Univariate Kruskal-Wallis tests and rank correlations (r_s) are included for each component, together with the Wilks' lambda (and Chi-square approximation) for the first discriminant function on all four components. Where there was no significant difference among vegetation classes for scores along a particular component, the K tests are denoted NS. Rank correlations significant at p = 0.05 are underscored.

1) Kruskal-Wallis K-statistics for stand scores on each principal component have 3 degrees of freedom. The Chi-square approximation of Wilks' lambda has 12 degrees of freedom.
2) Kruskal-Wallis K-statistics for stand scores on each principal component have 4 degrees of freedom. The Chi-square approximation of Wilks' lambda has 16 degrees of freedom.

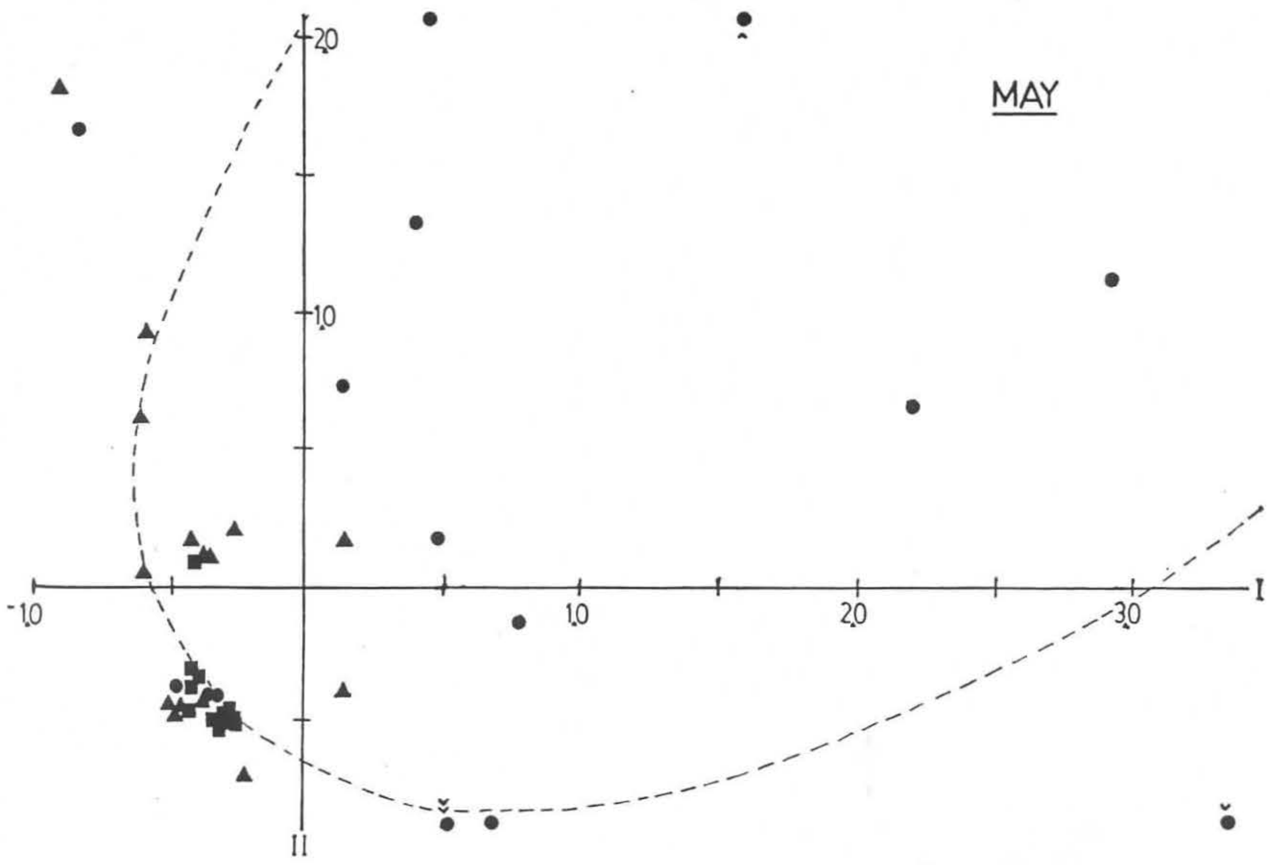


Fig. 1. Stand scores derived from Principal Component Analysis of collembolan abundance data prior to the use of Trend Surface Analysis ("pre-TSA"), May 1980. Closed circles, triangles, and squares represent 8, 4 and 2 year old plot samples respectively.

and September 1980 (Chi-square test of homogeneity, $p > 0.05$; mean $r_s = -0.390$, $p < 0.001$, $n = 135$). The remaining environmental variables were not significantly correlated ($p > 0.05$) with the sample scores. The lack of correspondence between the "q-scores" and spoil moisture content (and water potential) was likely due either to an incorrect choice of initial species weightings or to changes in faunal environment relationships between field seasons. The results of the correlation analysis suggested that direct gradient analysis was not the most suitable method of analyzing the Collembola data sets.

The results of the ensuing indirect gradient analysis conducted on the screened collembolan data sets have been summarized in Tables 3, 4, and 5, Figures 1, 2, and 3, and Appendix I. Only 5 of 14 species remained after the data screening procedure: *Hypogastrura denticulata*, *H. manubrialis*, *Folsomia nivalis*, *Onychiurus subtenius*, and *Isotoma cf. manitobae*.

Generally, changes in densities of the five species with respect to spoil moisture and organic matter were not monotonic; however, a significant, planar response surface was generated for *H. manubrialis* density data collected in September 1980. Differing orders of response surfaces were required to detrend the remaining species for the effects of variation in spoil moisture and organic matter content (Table 3). Only *O. subtenuis* displayed significant dependence upon the two environmental variables throughout the 1980 field season. The response surfaces generated by TSA were characterized by one or more density peaks; the predicted densities, together with moisture and organic matter data as coordinates of these peaks, have also been included in Table 3. When translated into water potentials using the equations provided in Table 2, the moisture-organic matter combinations were equivalent to moisture stresses from < -250 MPa to -0.03 MPa. (June spoil moisture contents were converted to water potentials using the regression equation derived from the July environmental data set.) The euedaphic species, *O. subtenuis*, tended to have higher peak densities at higher spoil water potentials than hemiedaphic species such *H. denticulata*. The predicted

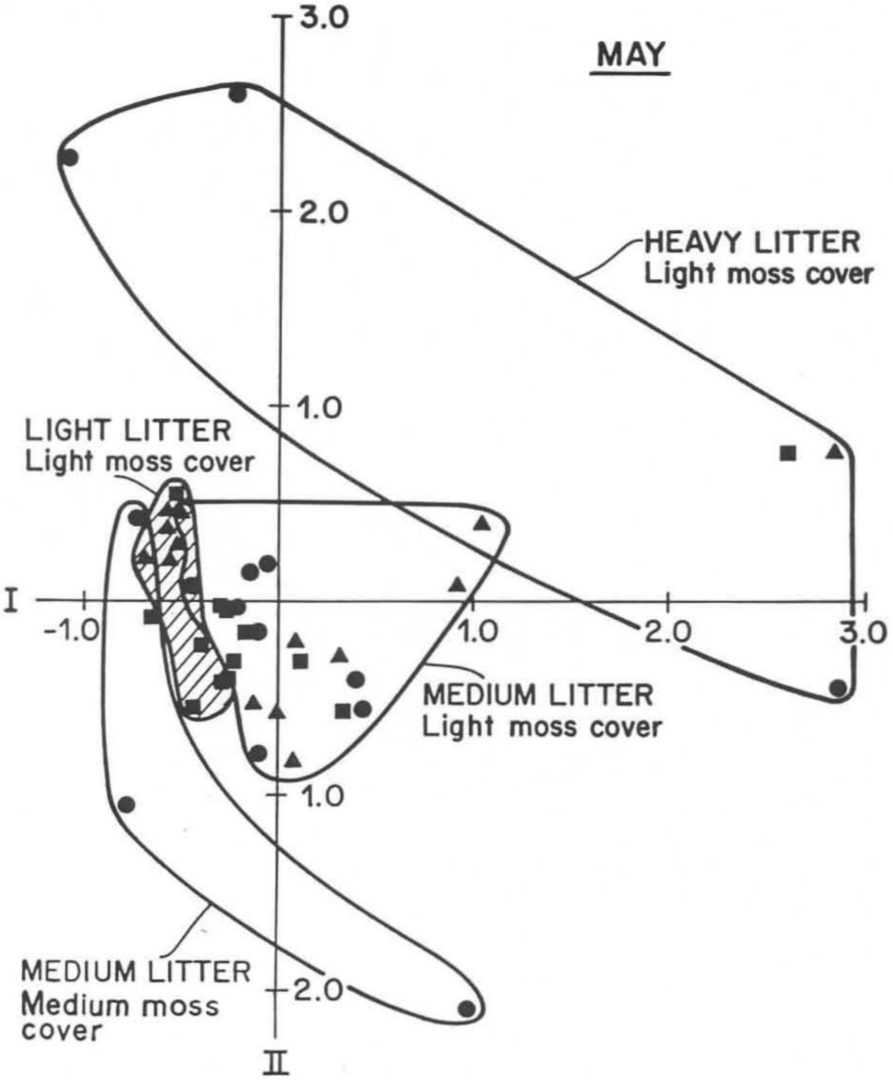
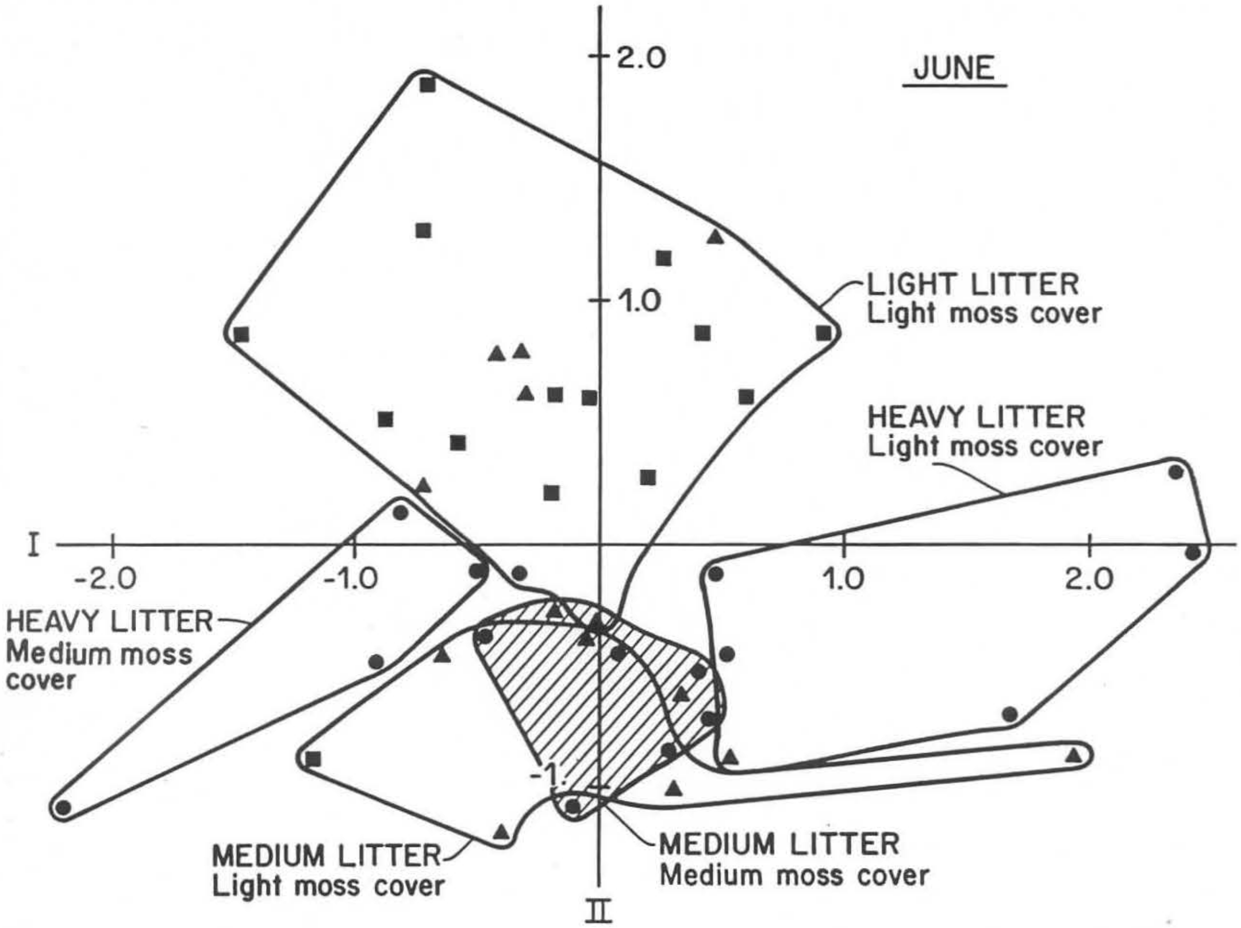


Fig. 2. Stand scores derived from Principal Component Analysis of collembolan abundance data after the application of Trend Surface Analysis ("post-TSA"), May 1980. Clusters of samples are based on original ranks assigned to litter cover and moss cover.

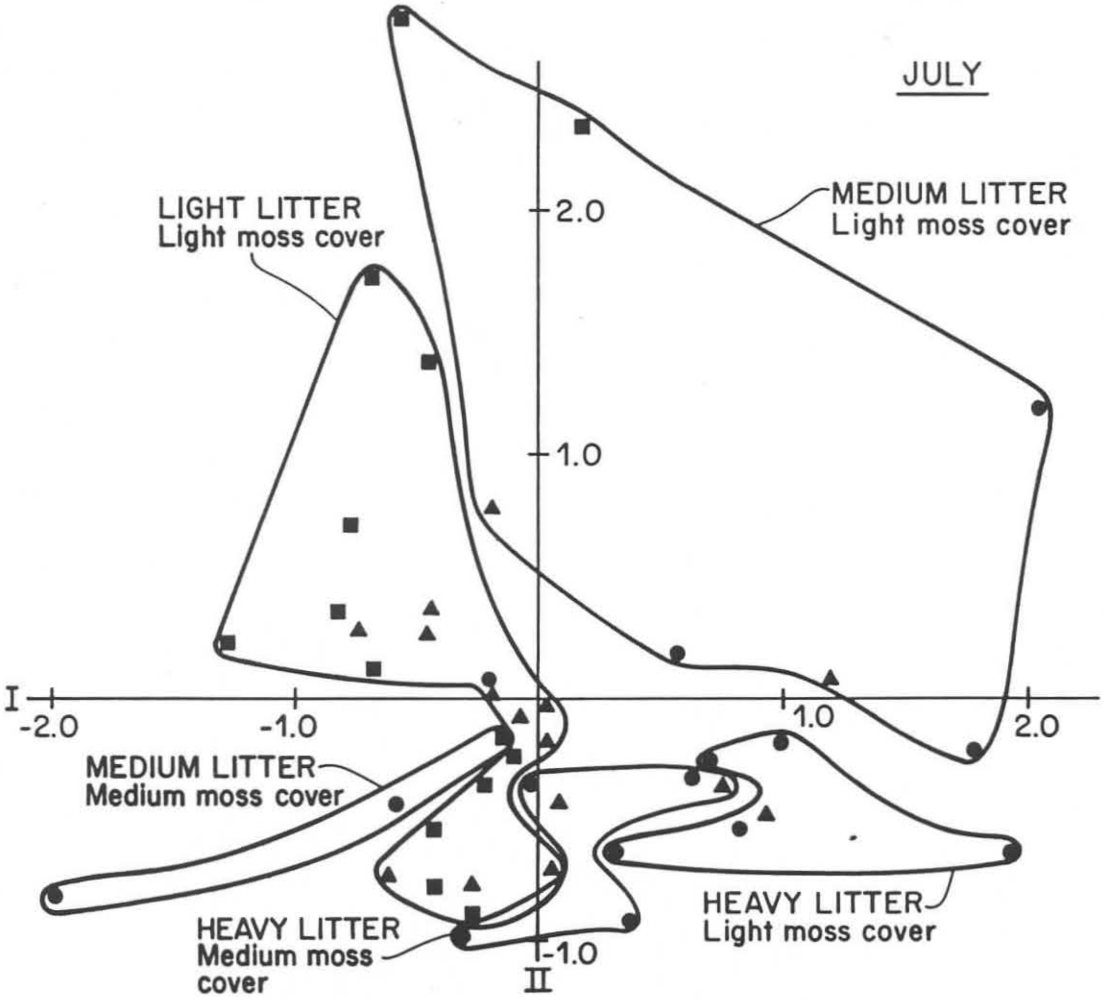
peak densities, pooled for all species, were significantly correlated ($r_s = -0.95$, $p < 0.001$, $n = 22$) with predicted water potential values.

As realistic trends can be extracted from random data, DAVIS' (1973) rule-of-thumb regarding the magnitude of the product-moment correlation coefficient associated with a trend surface equation was adopted as a second criterion (in addition to the F-statistic) for selecting significant regressions (cf. Section 3.2). The correlations have been included in Table 3. Equations with significant correlation coefficients < 0.30 were rejected as spurious relationships, and therefore, do not appear in the table. Coefficients 0.30 to 0.70 suggested cautious interpretation of trends and residuals, while equations with correlation coefficients > 0.70 were regarded as conforming closely to the original data points (DAVIS 1973).

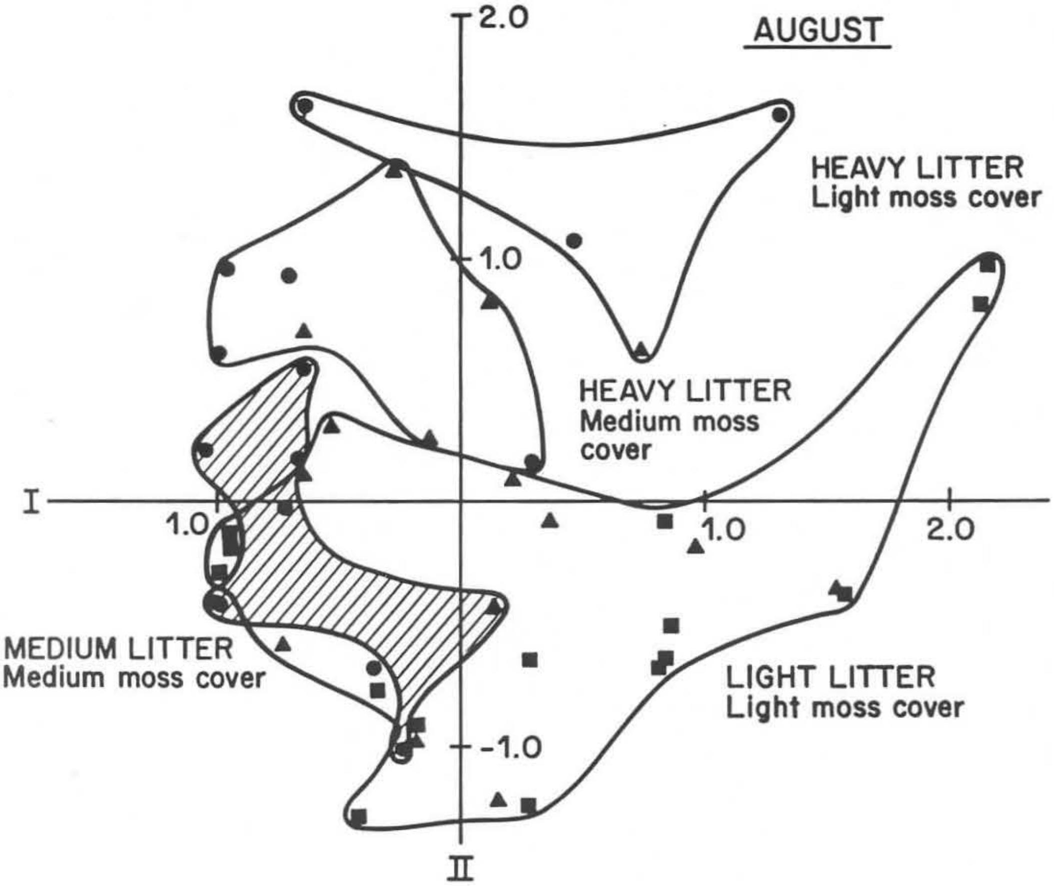
The species ordinations for the screened data sets have been summarized in Appendix I. Approximately 84% to 98% of total variation was accounted for by the first and second components in the "pre-TSA" species ordinations, while only 75% to 89% of the variance was similarly accounted for in the complimentary analyses conducted on the normalized trend surface residuals (i.e. the "post-TSA" ordinations). About 11% to 25% of the variance in the "post-TSA" species ordinations was distributed among principal components III and IV. In the "pre-TSA" ordinations, *H. denticulata* and *H. manubrialis* had high positive loadings on the same component. *Folsomia nivalis* and *O. subtenuis* were similarly paired on a second component. *Isotoma cf. manitobae* usually had positive loadings on still a third component. There was no consistent grouping of species loadings derived from the "post-TSA" ordinations.


JUNE
2.0
1.0
-1.
I
-2.0
-1.0
1.0
2.0
II
LIGHT LITTER
Light moss cover
HEAVY LITTER
Light moss cover
HEAVY LITTER
Medium moss cover
MEDIUM LITTER
Light moss cover
MEDIUM LITTER
Medium moss cover

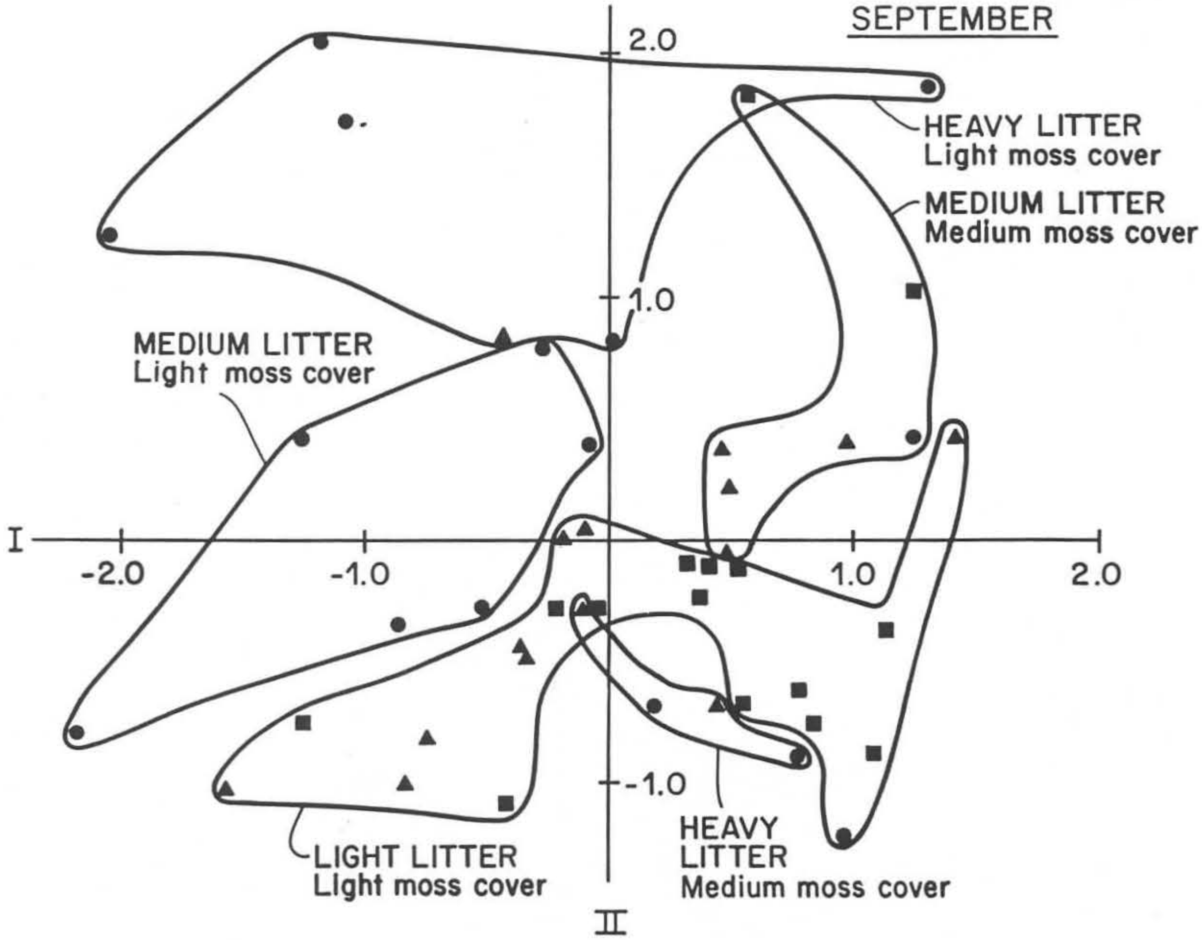
a


JULY
2.0
1.0
-1.0
I
-2.0
-1.0
1.0
2.0
II
LIGHT LITTER
Light moss cover
MEDIUM LITTER
Light moss cover
MEDIUM LITTER
Medium moss cover
HEAVY LITTER
Medium moss cover
HEAVY LITTER
Light moss cover

b



c



d

Fig. 3. "Post-TSA" stand ordinations of collembolan abundance data, June, July, August and September 1980. Symbols and clusters are the same as those described in Figs. 1 and 2.

VARIMAX rotation of the "post-TSA" species ordinations typically required 17 to 19 iterations to converge upon the terminal orthogonal solutions. About 35 to 45 iterations were necessary to achieve comparable rotation of the "pre-TSA" species ordinations. The VARIMAX procedure maximizes eigenvalues, i.e. the column sum of squared loadings representing each factor; however, variation within species accounted for by each of the principal components was not maximized. Variation in the row sums of squared loadings, i.e. communality estimates, suggested that the data partitioning procedure used in the present study did not behave in a consistent fashion from month to month (Appendix I). However, the advantage gained by detrending the species abundance data using TSA can be more fully appreciated in a comparison of Figs. 1 and 2.

Species loadings were used to produce stand factor scores, plotted in the reduced "species" or "community" space (*sensu* GAUCH 1982) as depicted in Figs. 1 and 2, and Fig. 3. Although not shown in any figure or table, ordinations produced from the data sets which had not undergone the editing procedure were characterized by "horseshoeing", i.e, extreme in-turning or involution of the endpoint stands. The "pre-TSA" stand ordinations were less affected by involution than by curvature or "arching" of the ordination as exemplified by the May data set depicted in Figure 1; the companion "post-TSA" ordination (Fig. 2) illustrated substantial reduction of the quadratic distortion imposed by the first principal component upon the second. Typically, the projections of factor scores into two-component space in subsequent monthly "post-TSA" stand ordinations also exhibited apparent reduction in quadratic distortion (Fig. 3). However, July and August ordinations were least affected by quadratic distortion; the first principal components of "pre-TSA" and "post-TSA" stand ordinations were highly, and positively correlated (July, $r_s = 0.78$, $p < 0.001$, $n = 45$; August, $r_s = 0.96$, $p < 0.001$, $n = 45$).

Rank correlations between the environmental variables and stand scores indicated that species abundances had been effectively detrended for spoil moisture and organic matter (as well as water potential) by the TSA conducted in all months (Table 4). On the other hand, predicted sediment densities were significantly rank correlated ($p < 0.05$) with principal component I (PC I) for all months, and principal component II for July through September ("pre-TSA") ordinations. Predicted sediment densities were correlated with at least one principal component for "post-TSA" stand ordinations from June to September (Table 4).

Vegetation classes have been superimposed upon the first two principal components of the "post-TSA" ordinations depicted in Figs. 2 and 3. The ordinated residuals were separated into 4 (or 5) significantly different groups along at least one of the components in the reduced community space (Table 5, Wilks' lambda likelihood ratios, $p < 0.05$). Components III and IV were not depicted in the figures. The significant Wilks' lambda for the first discriminant function derived from the May data was likely due to inequality among the group variance-covariance matrices (Box's M, approximate $F_{10 \cdot 1032} = 2.744$, $p < 0.001$). In subsequent months, the assumption of homogeneity among group variance-covariances was not as seriously violated (Box's M, $p > 0.01$). On the other hand, vegetation classes were not significantly different ($p > 0.05$) on every component according to univariate Kruskal-Wallis tests of the ranked stand scores, and in spite of the presence of occasional significant linear relationships between the two variables (Table 5, Spearman r_s, $p < 0.05$). Vegetation classes and stand scores were significantly correlated in June (PC II, III), July (PC I, II), August (PC II), and September (PC II, III).

5. Discussion

It has been observed that microarthropods are more frequently found in rhizospheres of individual plants in nutrient-poor soils, with the suggestion that microarthropod species composition is ultimately dependent upon the physiological characteristics of the individual plant species themselves (BLACKITH 1974). However, collembolan and acarine survival may simply depend on the ameliorating effects that vegetation cover exerts on soil temperature and moisture stress. In Antarctic polar desert. JANETSCHEK (1967) found that the relative

humidity of bare soil at 1 to 2 cm depth was 50% while adjacent moss cushions remained at 70% R. H. ADDISON (1980), using Polar Ordination, concluded that plant physiognomy was the primary determinant of collembolan species composition and abundance under individual tundra plants regardless of species. Differences in mean soil moisture content among the three categories of plants studied were most pronounced on a raised tundra beach ridge, the driest of her three study sites (ADDISON 1975). The three plant categories, *Dryas*, saxifrage, and crustose lichens, had very different growth forms. Moisture levels under *Dryas* were intermediate between saxifrage and crustose lichen; seasonal mean water potential 10 cm under *Dryas* was —2.0 MPa, with a seasonal low of —2.7 MPa (ADDISON 1977). These values were similar to water potential estimates made in the present study.

From a study of microarthropod populations associated with the root systems of individual pasture grass and weed species, CURRY & GANLEY (1976) also concluded that the relationship between the vegetation and the soil fauna should be considered more of a microclimatological phenomenon rather than a species-specific association determined by root physiology and rhizosphere microbiology. In a similar fashion, GODDARD (1979a, b) classified sample cores on the basis of presence or absence of lichens and moss prior to performing Principal Coordinate Analysis on the microarthropod data obtained from maritime Antarctic moss-turf communities. Although he effectively increased the number of "species" analyzed in the ordination by dividing each taxon (including the collembolan *Cryptopygus antarcticus*) into different size classes, the analysis did not reveal clear cut groupings in faunal species related to vegetational composition. However, species abundance was affected by the type of plant cover from core to core. The "pre-TSA" stand ordinations produced from the Luscar data sets bear certain similarities to GODDARD's Principal Coordinate diagrams, even though the species abundance data were not broken down by size and age class in the present study.

Multiple Discriminant Analysis proved useful in crudely delimiting the niches of the five species ordinated in the present study on the basis of vegetation classes. A formal analysis of niche breadth and overlap was deemed inappropriate owing to the unequal proportions of the resource categories used (i.e. vegetation classes). These coarse habitat measurements were more useful in the present study than detailed microhabitat analysis since the patchy distribution of vegetation and the associated soil fauna was reinforced by extreme fluctuations in temperature and moisture, and by restricted patterns of litter fall and redistribution which often characterize adverse environments.

Despite the use of Trend Surface Analysis to separate major sources of variation in the species abundance data, soil organic matter (as correlated with predicted sediment density) and spoil water potential remained important influences on the distribution and abundance of the five species. For example spoil *p*H was correlated with stand scores in May and July "post-TSA" ordinations. Soil *p*H can affect rates of ionic exchange between the soil solution and particles. Soil solutions became concentrated as spoil moisture decreased during the field season. Despite low specific conductance reported by VISSER *et al.* (1979), dissolved salts likely exerted substantial osmotic stress upon the Collembola colonizing Luscar spoil. The density of one species, *Isotoma ekmani* FJELLBERG, was significantly correlated with *p*H (PARSONS & PARKINSON 1986), but the osmotic and matric components of spoil water potential could not be differentiated using psychrometric methods. Thus, edaphic variables likely assumed as great an importance as litter cover in influencing collembolan abundance among microsites characterized by abrupt transitions between favourable and less-favoured habitat conditions.

Lithic material and aspect are the primary factors controlling surface temperatures on mine spoils in the Rocky Mountains (HARRISON 1974); HARRISON (1974) noted a 17 °C difference between south-and north facing slopes with 26° slopes, with the former exhibiting ground surface temperatures as high as 52 °C. In the present study, surface temperature maxima of 40 °C to 60 °C were recorded beneath moderate litter cover ("medium litter-medium moss") on the 8 year old plot, while maxima ranged from 30 °C to 50 °C on mineral soil on the more northerly facing 4 and 2 year old plots (W. F. J. PARSONS, unpublished data). These values are comparable to surface temperatures recorded on bare spoil heaps

in central Pennsylvania (DEELEY & BORDEN 1973) and England (RICHARDSON 1958), as well as clear-cut areas of subalpine forest adjacent to Luscar (DAY 1963).

In a study of seedbed characteristics and germination success on Luscar spoil, DILLON (1973) found that even slight microtopographic variation could greatly influence the substrate temperature as well as moisture stress regimes of adjacent sampling sites. He also determined that spoil moisture content of shaded hollows was twice as high as moisture levels on exposed rises held at the same moisture tension, due primarily to redeposition of fine-textured materials in the depressions from upslope sites. Alteration of spoil moisture retention characteristics by redeposition of sediments was also observed in the present study.

Soil moisture storage, depletion, and recharge depend on the complex interplay of topography, soil porosity and permeability, the distribution and physiological status of the vegetation cover, as well as meterological phenomena. As water potential decreases below —1.5 MPa, water movement in the vapour phase assumes increasing importance (ROSE 1968); vapor diffusion in very dry soils, such as mine spoil, subject to marked fluctuations in surface temperature may lead to great differences in water potential over very short distances as cooling or heating proceeds.

The clusters of stands which emerged from the ordinations, together with results of the Multiple Discriminant Analysis, suggested that grouped stands shared similar assemblages of species or "component communities" (*sensu* ROOT 1973), despite wide differences in geographical location of the individual sample cores around the Luscar dump site. According to ROOT (1973), a habitat patch possesses unique properties associated with characteristics of the local environment which generate, in turn, a predictable subunit of the greater community (*viz.* the component community). The component community responds not only to the physical and chemical characteristics of the habitat patch, and to the level and constancy of available resources, but also to the durational stability of the patch itself (SOUTHWOOD 1977). It follows that the magnitude and direction of ecosystem-level transfers of energy and nutrients vary among component communities. Extrapolating from ROOT's definition of "component communities", REICE (1974) proposed that community level processes, such as decomposition, should vary along environmental gradients, i.e. from patch to patch. He determined that leaf litter disappearance within streams varied with the type and size of habitat patches along a velocity-sediment gradient; leaf pack size was also a very important determinant of litter breakdown in lotic systems. WHITFORD *et al.* (1980) advanced a similar hypothesis for a terrestrial ecosystem, Chihuahuan desert. They found that microarthropod abundance was directly proportional to the amount of surface litter present (SANTOS *et al.* 1978) and as a consequence, in direct proportion to the rate of decomposition occurring in exposed creosote bush *(Larrea tridentata)* litter. In contrast with studies of litter colonization and decomposition conducted in desert (e.g. FRANCO *et al.* 1979; VOSSBRINCK *et al.* 1979; SANTOS *et al.* 1981), and mesic forest systems (e.g. STANTON 1979; SEASTEDT *et al.* 1983), Collembola were the major colonists of the buried litter bags extracted in the present study; 97% of these microarthropods consisted of one species, *Hypogastrura denticulata*.

In the present study, stand scores derived from the ordinations were significantly and positively correlated with vegetation class and predicted sediment density. In addition species number was significantly and negatively correlated with predicted sediment density, and collembolan abundance in the buried litter bags was positively correlated with actual sediment density. As in the Chihuahuan desert, Luscar mine spoil was subject to high surface temperatures, sheet surface runoff, wind scouring, and intermittent burial of litter. In addition to litter burial, litter was probably redistributed to a certain extent by wind and surface runoff; light litter cover tended to be associated with high microrelief. The patchy distribution of litter can also be related to the ease with which vegetation is established on mine spoils with various angles of repose. ETTER (1971, in DILLON 1973) found that germination success decreased exponentially as slope angle increased. Above 26° to 34° (i.e. slope class value of 8), mine spoil was too unstable to allow sufficient numbers of grass and legume seedlings to take root and thus, prevent further erosion. DILLON (1973) speculated that the marked reduction in germinant coverage was due to erosion of the seed bed prior to germination,

lack of moisture due to increased runoff, and seedling mortality due to abrasion by runoff and colluvium. When continual mechanical weathering was also taken into consideration, the correspondence between light moss cover and high slope class values (i.e. 7 to 8) suggested that differences in moss cover in the present study were due to instability of the supporting substrate as well as low moisture levels. Thus, it was quite likely that new microsites were being continually created while old patches were destroyed by ongoing erosional processes.

Physical disturbance has been considered responsible for maintaining the mosaic character of many communities (LEVIN & PAINE 1974; SOUSA 1984). It has been suggested (LOUCKS 1970) that species diversity increases when disturbance maintains competitively inferior species (i.e. fugitive species) which survive by colonizing newly disturbed patches. The hypothesis has been advanced (CONNELL 1978) that diversity is maximized by intermediate levels of disturbance, and that only fugitive species, such as *H. denticulata* survive under high disturbance regimes.

6. A postscript on ordination in soil faunal research

Ideally, ordination algorithms should make provisions both for non linear species response and for correlations between environmental gradients. While a direct comparison of species abundances (criterion variables) against physico-chemical variables (predictor variables) would appear to be the most logical procedure, this method of Canonical Correlation Analysis (CCA) is not robust to the departures from normality and linearity generally encountered in complex communities (GAUCH 1982). At the other extreme, Gaussian Ordination (GO) fits normal functions to species abundance data along environmental gradients (IHM & VAN GROENEWOUD 1975). While more realistic in the context of models of community organization, GO cannot be easily extended to more than one gradient when data display substantial non-systematic variation (GAUCH *et al.* 1974). In addition, the normal curves generated by GO poorly approximate more skewed and multimodal data.

The most efficient and biologically meaningful method of ordinating community data sets lies between the extremes of common factoring techniques and complex, non-linear manipulations such as GO. A suite of techniques, under the umbrella of Catenation (GAUCH 1982), can be brought into play to maximize the analytical power of the established factoring methods: distortions in the orthogonal components or abstract axes can be removed by: Parametric Mapping (NOY-MEIR 1974), Polynomial Ordination (PHILLIPS 1978), and Detrended Correspondence Analysis (HILL & GAUCH 1980). CARLETON (1984) has improved upon JOHNSON's (1981) technique by combining Detrended Correspondence Analysis with Canonical Correlation. He has formalized the procedure for simultaneously partialling-out unique variation in species abundance data while conducting the Canonical Correlation Analysis upon environmental data and ordinated community data sets as Residual Ordination Analysis. In this way, he has obviated the problem of correlation between gradients that plagued earlier attempts at indirect gradient analysis. Soil biologists should avail themselves of the technique, since certain problems, e.g. microarthropod aggregation, have not been satisfactorily explained. Field data suggesting dependence of soil faunal populations on water availability, and laboratory experiments demonstrating food preferences may be manifestations of the same influence: preferred foods may grow best at a particular field water content (USHER 1976). Detrending procedures could help elucidate relationships between the soil microarthropods and the microflora upon which they feed. If microarthropod and microbial data matrices were both detrended for some common source of variation, it might be possible to summarize competitive or predator-prey relationships within a multivariate space of few dimensions.

7. Acknowledgements

The authors would like to thank officials of Cardinal River Coals Limited for allowing access to the Luscar mine site. Comments on the manuscript by B. R. TAYLOR and L. R. LINTON were greatly appreciated. The work was supported by a Natural Sciences and Engineering Research Council operating grant to D. PARKINSON.

Appendix I Summary of Principal Components Analyses of screened monthly Collembola data sets, May to September 1980

Month		pre-TSA I	pre-TSA II	pre-TSA III	pre-TSA h²	post-TSA I	post-TSA II	post-TSA III	post-TSA IV	post-TSA h²
May	HYDE	0.411	0.732	0.165	0.732	0.807	—0.260	0.153	0.236	0.789
	FONI	0.876	0.269	0.118	0.850	0.155	0.155	—0.161	0.629	0.470
	ONSU	0.692	0.169	0.397	0.665	—0.034	0.695	0.272	0.195	0.596
	ISMA	0.129	0.146	0.427	0.220	0.046	0.227	0.659	0.170	0.518
	HYMA	0.074	0.607	0.105	0.386	0.807	0.136	0.055	0.054	0.675
	λ	1.862	0.798	0.192		1.442	0.873	0.591	0.151	
	%	65.3	28.0	6.7		47.2	28.6	19.3	4.9	
June	HYDE	0.767	—0.012	—0.238	0.646	—0.156	0.579	—0.269	0.263	0.501
	FONI	—0.167	0.900	0.215	0.884	0.802	—0.191	0.265	0.163	0.777
	ONSU	—0.043	0.629	0.157	0.423	0.818	—0.020	0.076	—0.166	0.703
	ISMA	—0.019	0.270	0.644	0.487	0.107	—0.030	0.487	—0.017	0.250
	HYMA	0.845	—0.189	0.212	0.795	—0.033	0.654	0.047	—0.081	0.473
	λ	1.787	1.073	0.374		1.615	0.686	0.250	0.117	
	%	55.2	33.2	11.6		60.5	25.7	9.4	4.4	
July	HYDE	0.019	0.671	0.477	0.679	0.021	0.656	0.521	0.161	0.729
	FONI	0.765	—0.092	0.191	0.631	0.667	—0.118	0.161	0.161	0.511
	ONSU	0.799	0.078	0.093	0.653	0.678	0.065	0.167	—0.144	0.512
	ISMA	0.185	—0.019	0.628	0.429	0.338	0.075	0.658	—0.017	0.553
	HYMA	—0.018	0.800	—0.148	0.662	—0.039	0.726	0.005	—0.598	0.553
	λ	1.438	1.137	0.478		1.480	1.021	0.270	0.065	
	%	47.1	37.2	15.7		52.2	36.0	9.5	2.3	
August	HYDE	0.815	—0.149	0.211	0.731	0.821	—0.121	0.251	—0.050	0.755
	FONI	0.052	0.752	—0.064	0.573	0.013	0.676	—0.025	0.160	0.484
	ONSU	—0.186	0.683	0.049	0.503	—0.142	0.390	0.041	0.550	0.477
	ISMA	0.402	—0.050	—0.033	0.165	0.251	—0.027	0.473	0.031	0.289
	HYMA	0.945	0.026	—0.107	0.905	0.782	0.191	0.431	—0.333	0.945
	λ	1.814	1.003	0.060		1.826	0.807	0.208	0.107	
	%	63.0	34.9	2.1		61.9	27.4	7.1	3.6	
September	HYDE	—0.006	0.797	0.212	0.679	0.780	0.258	0.125	0.392	0.845
	FONI	0.803	0.081	—0.152	0.674	—0.010	0.766	—0.010	—0.086	0.595
	ONSU	0.744	—0.260	0.186	0.656	—0.733	0.383	0.342	—0.003	0.801
	ISMA	0.021	0.178	0.329	0.141	—0.066	0.005	0.607	0.197	0.412
	HYMA	—0.212	0.604	0.387	0.559	0.200	—0.146	0.312	0.625	0.549
	λ	1.522	1.003	0.184		1.436	0.949	0.736	0.080	
	%	56.2	37.0	6.8		44.9	29.7	23.0	2.4	

Component loadings and communalities (h²) are given for each species, together with eigenvalues (λ) and variance explained by each component (%).

Note: Species codes = HYDE *Hypogastrura denticulata*; FONI *Folsomia nivalis*; ONSU *Onychiurus subtenuis*; ISMA *Isotoma cf. manitobae*; HYMA *Hypogastrura manubrialis*

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Synopsis: *Original scientific paper*

PARSONS, W. F. J., & D. PARKINSON, 1985. The use of data-partitioning in the ordination and gradient analysis of a collembolan community. Pedobiologia **29**, 91—111.

During May to September 1980, 14 species of Collembola were collected from three reclaimed, subalpine coal mine spoils differing in age since reclamation (8, 4, and 2 years). Five of the species were subsequently used in a community level study employing gradient analysis and ordination (Principal Components Analysis). The ordinations were constructed from the screened species abundance data prior to, and after curvilinear regression analysis (Trend Surface Analysis) on spoil moisture and organic matter content. The Trend Surface Analysis was intended to detrend the collembolan density data with respect to a gradient of soil moisture stress. The residual variation displayed much less pronounced distortion ("arching") when ordinated in a reduced data space then the species abundance data which had not been subjected to regression analysis prior to ordination. Factor scores obtained from the ordination of the residuals were related to the density of litter and moss cover by Multiple Discriminant Analysis, and were indicative of microsite stability. The factor scores were also significantly correlated with a gradient of erosion potential.

Data-partioning techniques could not completely separate the highly correlated components of the complex-environmental gradient of water potential, but Trend Surface Analysis, when combined with PCA, was a more useful strategy of delimiting habitat utilization in the Collembola than the direct application of ordination to the faunal data sets.

Key words: Collembola, gradient analysis, Principal Components Analysis, Trend Surface Analysis, data partitioning, mine spoil reclamation.